

Two-hundred year record of increasing growth rates for ocean quahogs (*Arctica islandica*) from the northwestern Atlantic Ocean



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ABSTRACT

Ocean quahogs [*Arctica islandica* (Linnaeus, 1769)] are the longest-lived, non-colonial animal known today, with a maximum life span exceeding 500 years. Ocean quahogs are a commercially important bivalve, inhabiting the continental shelf of the North Atlantic basin. We examined growth rates of ocean quahogs that were fully recruited to the commercial fishery (> 80-mm shell length) from four sites covering the range of the stock along the east coast of the U.S. through analysis of annual growth lines in the hinge plate. Both geographic and temporal differences (on a scale of decadal or longer) in growth rates exist throughout the range of the stock. The age at which animals reached 60, 80, and 90 mm decreased significantly, and average growth rates to 60, 80, and 90 mm increased significantly with birth year at a New Jersey and a Long Island site, both located in the southwestern portion of the stock, since the late 1700s/early 1800s, likely in response to increasing bottom water temperatures. That is, growth rates vary temporally with birth date at the southwestern sites, with younger animals growing at a much faster rate in recent decades than those born many decades previously, whereas at the northern sites off southern New England and on Georges Bank, changes in growth rates through time are limited to older adult animals or absent altogether. Thus, at the southern portion of the range, variation in growth rate over time exists in all phases of ocean quahog life, whereas on Georges Bank, little evidence exists for any differential in growth rate over the last ~200 years. The fact that ocean quahogs record the rise in ocean temperatures after the Little Ice Age in the Mid-Atlantic Bight southeast of southern New England, yet demonstrate little evidence of such a rise in the southern New England and Georges Bank region, would suggest a differential response of ocean circulation and its control of bottom water temperature between the northern and southern portions of the Mid-Atlantic Bight over the last 200+ years.

1. Introduction

The ocean quahog, *Arctica islandica*, is a widespread, biomass dominant on the continental shelf throughout the northwestern North Atlantic (Merrill and Ropes, 1969; Cargnelli et al., 1999; Dahlgren et al., 2000). These bivalve molluscs grow slowly to a shell length of about 130-mm, with a life span capable of exceeding 500 years (Butler et al., 2013). The long life span and the sensitivity of the species to interannual variations in the environment, particularly temperature, have supported the use of time series of growth as a temperature proxy to track long-term trends in climate (Schöne et al., 2003; Butler et al., 2010; Butler et al., 2013) and shorter term climate cycles (Schöne et al., 2005a; Butler et al., 2013; Lofmann and Schöne, 2013; Beierlein et al., 2015). In addition to the importance of this clam as a benthic biomass dominant and its value in elucidating long-term trends in climate, the ocean quahog also supports a commercial fishery that provides clam

meat for most commercial chowders. Indeed, a commercially valuable fishery for this species has existed in the U.S. since the late 1960's (NEFSC, 2009, 2017a). An essential element in the sustainable management of this fishery is information on growth rate, which controls the age at which animals reach a size that can be selected by the commercial dredge.

The growth of ocean quahogs varies substantially throughout the lifetime of an individual, and proceeds through ontogeny and into old age in a manner that is unlike the growth process of most other bivalves. Juvenile ocean quahogs grow rapidly, displaying near exponential growth until the onset of maturity, whereupon growth rate slows, yet growth continues throughout the lifetime of the individual. Although numerous authors have applied a von-Bertalanffy growth model to this species (e.g., Brey et al., 1990; Lewis et al., 2001; Kilada et al., 2007), the continuation of growth into old age contradicts the basic assumption of asymptotic growth in this model. Pace et al.

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(2017a) showed that an alternative growth model specified by Tanaka (1982, 1988) provides a better description of this growth dynamic by combining both the near exponential growth of the juvenile phase with the continuous indeterminate growth of the adult into old age.

Geographic differences in growth rates of ocean quahogs are also well documented (Murawski et al., 1982; Brey et al., 1990; NEFSC, 1995; Lewis et al., 2001; Thórarinsdóttir and Jacobson, 2005; Kilada et al., 2007; Ridgway et al., 2012). Witbaard et al. (1999) suggest that the regional differences in growth rates are predominantly due to differences in primary production, but it is certain that a combination of several environmental factors contribute to the varying growth rates throughout the range of the stock and, indeed, Marali and Schöne (2015), Mette et al. (2016), Reynolds et al. (2017) and others have shown that variations in growth of individual animals over their life span can be explained in part by changes in sea surface, and by inference, bottom water temperatures. Additionally, sex-related differences in growth rate of ocean quahogs have been described (Ropes et al., 1984; Steingrímsson and Thórarinsdóttir, 1995). Regardless of the mechanism behind variable growth rates of this species, the result is an inability to create a single age-length key for the species. Varying growth rates, observed throughout the range of the ocean quahog stock, produce not only regional differences in growth rate, but also differential localized growth rates such that a wide range in age at length is found throughout most of the post-juvenile phase of life (Pace et al., 2017b). Thus, any age-at-length key that might be developed from a local population could result in inaccurate age estimates for more distant populations of ocean quahogs (Pace et al. 2017b).

Characteristics of age and growth of various ocean quahog populations from the U.S. mid-Atlantic continental shelf have been described (Murawski et al., 1982; NEFSC, 1995; Lewis et al., 2001; Pace et al., 2017b), but the number and geographic scope of these studies is limited. In addition, variations in growth as a function of environmental change remain undescribed for this species in the northwest Atlantic, though one anticipates that such variations should exist, as the species is found at latitudes farther south off the U.S. coastline than elsewhere in its boreal circumambience (Merrill and Ropes, 1969; Dahlgren et al., 2000; for further documentation of the North Atlantic range, see Brey et al., 1990; Rowell et al., 1990; Witbaard et al., 1999; Ragnarsson and Thórarinsdóttir, 2002; Butler et al., 2009). Thus, a need for understanding the age-at-length relationships throughout the range of the U.S. stock exists to inform fishery management, provide a basis for age-structured stock assessment models, and also to elucidate regional shifts in ocean climate over the last few centuries. The objective of this study was to investigate growth rates of selected individuals from four ocean quahog populations covering much of the mid-Atlantic range of the stock through the analysis of annual growth increments. To do this, growth increment time series for animals covering the age range observed in the four populations were used to determine the age at 60-, 80-, and 90-mm, and the average growth rates from birth to 60 mm, 60 to 80 mm, 80 to 90 mm, and post-90 mm. These data were evaluated as a function of birth year, within and between populations, to elucidate regional trends in growth and uncover time-dependent trends in growth, should they exist.

2. Material and methods

2.1. Sample collection and preparation

Ocean quahog samples were collected from New Jersey and Long Island from the *F/V Christie* in March 2015 and from Southern New England and Georges Bank from the *F/V Pursuit* in May 2015 using hydraulic dredges (Fig. 1). Initially, five clams were arbitrarily selected from each 5-mm size bin starting with 80 mm through the maximum shell length (anterior-posterior) collected at each site. For the New Jersey and Long Island sites, an additional five clams were selected from each 5-mm size bin to better define trends in growth rate with

birth year. Clams were sectioned along the height axis (dorsal-ventral) using a modified commercial tile saw. Sectioned clams were ground and polished on a wet polishing wheel on 400-μm and 600-μm sandpaper grit, followed by 6-μm and 1-μm diamond suspensions on polishing pads. Additional details are provided by Pace et al. (2017a).

Images of the hinge region of all sectioned clams were captured using either a high definition Olympus DP73 digital microscope camera using the Olympus cellSens microscope imaging software or a high definition Olympus America microscope camera using Olympus MicroSuite software. Many photographs of the hinge region were required to produce a continuous image of the hinge at high magnification. Each individual image was automatically stitched together by the cellSens microscope imaging software. Hinge photographs taken using the Olympus MicroSuite software were stitched together using the open source software ImageJ (Fiji) to create a complete image of the hinge section. Through the use of the ObjectJ plugin in ImageJ, annual growth lines in the hinge region of each individual were annotated (see Fig. 2 in Pace et al. 2017b) and the growth increment widths (distance between consecutive annual growth lines) measured in units of pixels. The total shell length (mm) of an individual divided by the cumulative sum of all growth increment widths (pixels) provided a pixel-to-mm conversion.

2.2. Correlation analysis

Age estimates and measurements of growth increment widths were recorded for 205 individuals throughout the Mid-Atlantic [New Jersey (80), Long Island (65), Georges Bank (35), southern New England (25)]. Using this growth increment information, the age at which individuals reached 80 mm was compared to the year each individual was born. This shell length was initially selected because the capture efficiency of commercial dredges declines at clam lengths < 80 mm so that the abundance of smaller animals in the catch is not representative of their abundance in the population (NEFSC, 2017a); thus animals ≥ 80 mm are of a size of interest to the fishery and management of the species. To investigate whether any trends relating to birth year were specific to 80 mm, or if they held true throughout a larger size range, the ages at which animals reached 60- and 90-mm in shell length were also compared to the birth year of each individual. The 60-mm size was chosen because it approximates size at maturity (Rowell et al., 1990; Thórarinsdóttir and Jacobson, 2005; NEFSC, 2017a). The 90-mm size is a convenient size well within the adult length and age spans, but under the maximum size obtained at each of the four sites.

A Pearson's correlation test was used to test the strength of correlations between birth year and these variables at each site. Additional Pearson's correlation tests were used to test for correlations between birth year and shell length. Specifically, the variables examined were the average growth rate from birth to 60 mm, from 60 to 80 mm, from 80 to 90 mm, and the average growth rate from 90 mm to size at time of collection at each of the four sites. Hereafter, the former three average growth rates will be referenced by the upper size boundary, e.g., average growth rate from birth to 60 mm will be referred to as growth rate to 60 mm. The final growth increment from 90 mm to size at time of collection will be referred to as post-90 mm.

2.3. ANCOVA and regression analysis

Analyses of covariance and post-hoc least squares means tests were used to identify the relationship between the age at which animals reached each size (60, 80, 90 mm) and the intervening growth rates as a function of birth year and location. Each ANCOVA retained the interaction term if significant ($\alpha \leq 0.05$). We use ANCOVA because birth year is a discrete variable in this analysis rather than a main effect and thus serves as a covariate.

Multiple linear regression using the maximum R-square improvement method (Freund and Littell, 2000) was used to examine the ability

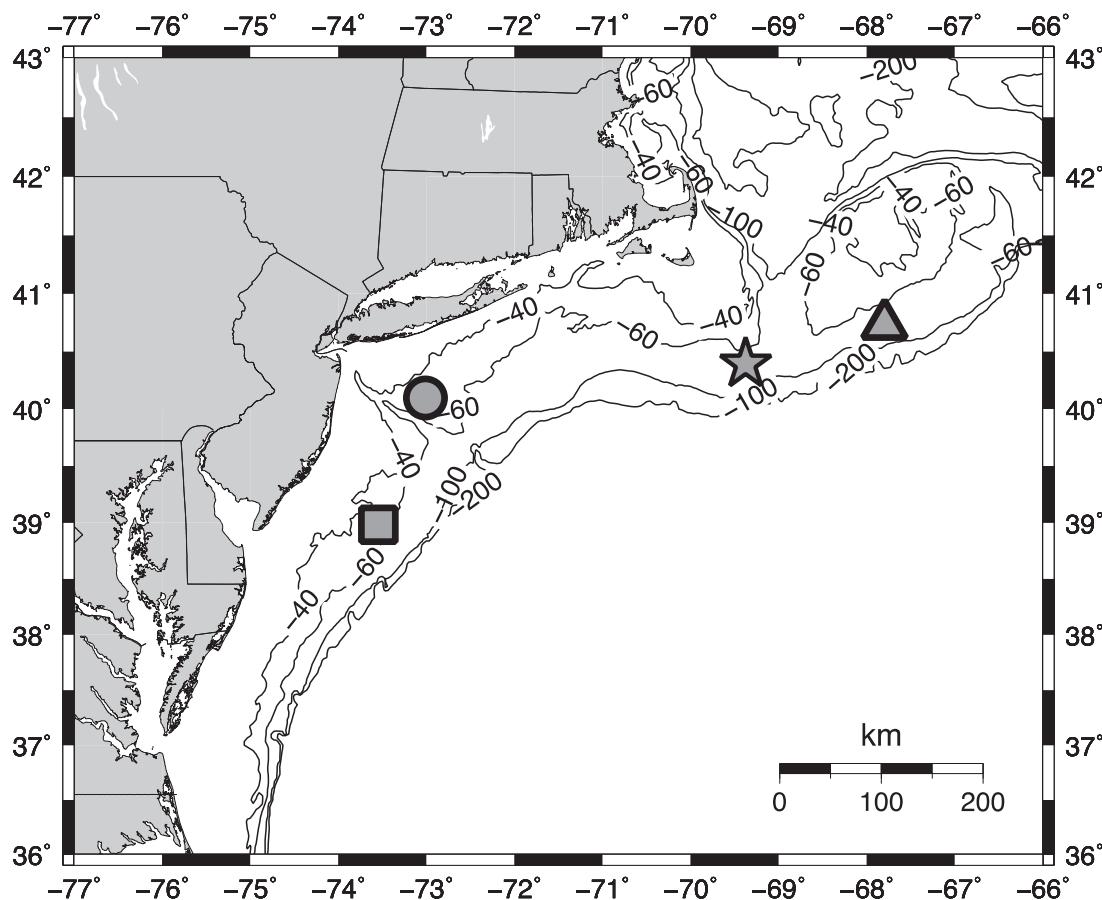


Fig. 1. Map of sample collection sites: New Jersey (square), Long Island (circle), Southern New England (star), and Georges Bank (triangle).

of growth-dependent variables to predict the birth year of an individual at each site. Shell length and average growth rate to 60 mm, 80 mm, 90 mm, and post-90 mm were used as independent variables. Significant regression models indicate that the growth process has varied over time at a site with sufficient directionality that the growth dynamics of an individual are in part determined by the year of birth. For a given age, the size at time of collection for an ocean quahog will be determined by the time required to reach maturity and the rate of growth as an adult. To further assess the importance of birth year, and to evaluate the relative importance of growth rate to maturity relative to adult growth, two additional regression models were investigated. The first limited the independent variables to those associated only with early growth rates, namely the average growth rate to 60 mm and to 80 mm. A second employed growth rates to 60 mm, 80 mm, and 90 mm. Animals that were < 90 mm at time of collection performed were omitted from this model. Many, but not all, of these animals were relatively young. Thus, this last regression model was biased in favor of animals born earlier in the time history of the population.

3. Results

3.1. Correlation analysis

Plots of age at 60, 80, and 90 mm versus birth year are shown in Figs. 2–3. A significant negative Pearson's correlation exists between birth year and age at 60 mm ($r = -0.567, p < 0.0001$), 80 mm ($r = -0.592, p < 0.0001$), and 90 mm ($r = -0.396, p = 0.0003$) at the New Jersey site and at the Long Island site [60 mm ($r = -0.745, p < 0.0001$); 80 mm ($r = -0.799, p < 0.0001$); 90 mm ($r = -0.634, p < 0.0001$)]; that is, at the two southern sites, as birth year increased, the age at which individuals reached 60, 80, and 90 mm decreased.

Thus older animals were characterized by slower growth rates to an equivalent size, including juvenile and adult growth. In addition, the correlations were consistently strongest at the Long Island site.

In contrast, at the Georges Bank site, neither the correlation between birth year and age at 60 mm nor at 80 mm was significant, but a significant negative correlation existed between birth year and age at 90 mm ($r = -0.429, p = 0.0102$). Similarly, at the Southern New England site, the correlations between birth year and age at 60 mm and 80 mm were not significant, whereas a significant negative correlation was observed at 90 mm ($r = -0.496, p = 0.0116$). Results of these correlation tests suggest that ocean quahogs born more recently grew at a faster rate than older clams at the two southern sites, whereas at the two northern sites, the year that individuals were born had little effect on early growth rates and thus little effect on the age at which animals reached 60 or 80 mm. Growth rates of older adults, however, had a significant correlation with birth year, as shown by the growth rate between 80 and 90 mm and the correlation coefficients were stronger for the two northeastern sites than for the most southern site off New Jersey, but still lower than for the Long Island site.

At all four sites, a significant correlation existed between birth year and total shell length [New Jersey ($r = -0.790, p < 0.0001$), Long Island ($r = -0.789, p < 0.0001$), Georges Bank ($r = -0.789, p = 0.601, p = 0.0001$), Southern New England ($r = -0.613, p = 0.001$)], indicating that, in general, larger clams tended to be older. That is, the change in growth rates observed with birth year were not sufficiently intense that the younger clams, born more recently and growing at higher rates, were larger at the time of collection than the older clams, born earlier and growing at slower rates at the same time in their life history.

Plots of average growth rate to 60, 60–80, 80–90, and post-90 mm versus birth year are shown in Figs. 4–6. Significant positive

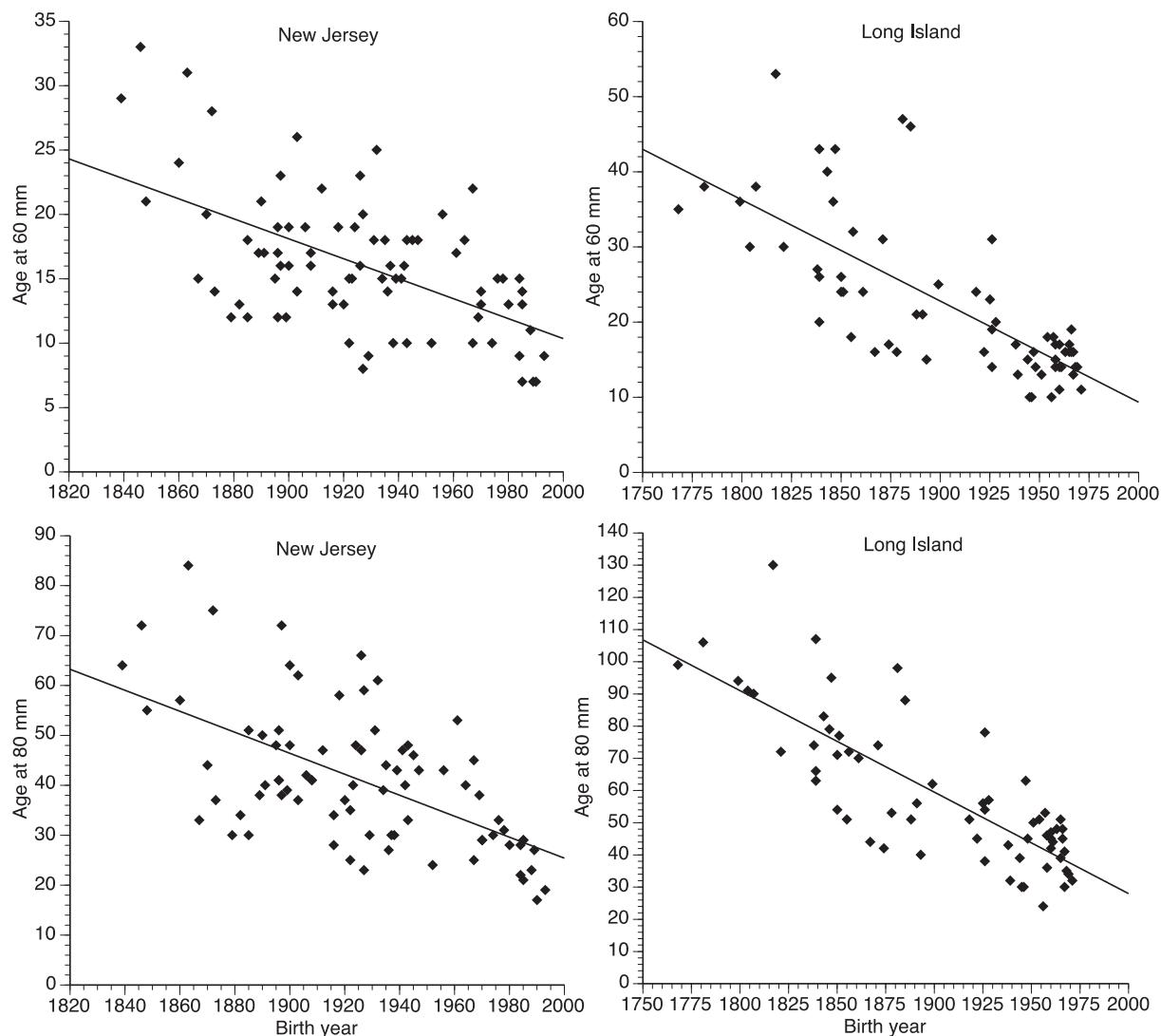


Fig. 2. Top: birth year versus age at 60 mm. Bottom: birth year versus age at 80 mm. Regression lines indicate significant regressions ($P \leq 0.05$).

correlations exist between birth year and growth rates to 60 mm ($r = 0.539$, $p < 0.0001$), 80 mm ($r = 0.602$, $p < 0.0001$), 90 mm ($r = 0.401$, $p = 0.0002$), and post-90 mm ($r = 0.500$, $p < 0.0001$) at the New Jersey site and at the Long Island site [growth rate to 60 mm ($r = 0.768$, $p < 0.0001$); 80 mm ($r = 0.516$, $p < 0.0001$); 90 mm ($r = 0.522$, $p < 0.0001$); and post-90 mm ($r = 0.516$, $p < 0.0001$)]; thus, at these two sites animals born more recently grew at faster rates in each of these phases of growth compared to animals born many decades previously, explaining the presence of a decreasing age at 60–90 mm as birth year increased. The trend is a product of lifetime growth at these two southern sites rather than, for example, differential growth rate at one specific life stage.

At the Georges Bank site, the only growth phase with a growth rate correlated with birth year was growth rate post-90 mm ($r = 0.562$, $p = 0.0004$). At the Southern New England site, whereas average growth rates to 60 and 80 mm were not significantly correlated with birth year, the growth rate to 90 mm ($r = 0.490$, $p = 0.0129$) and post-90 mm ($r = 0.561$, $p = 0.0035$) were both significantly correlated with birth year. These correlations explain earlier results in the comparison of birth year to age at which animals reach 90 mm, in that growth rates only appear to increase with more recent birth years after animals reach 90 mm in size at the Georges Bank site, whereas growth rates began to increase after animals reached > 80 mm in length at the Southern New England site, resulting in the significant negative correlation between

age at 90 mm and birth year at the two northern sites. Of note is the strong tendency for early growth rates to be less affected by birth year at higher latitudes, with an increasing restriction of this differential to increasingly older animals at progressively more northeastern locations.

3.2. ANCOVA

For age at 60 mm, the main effect of location ($F = 5.87$, $p = 0.0007$), the covariate birth year ($F = 16.65$, $p < 0.0001$), and the interaction term ($F = 5.71$, $p = 0.0009$) were all significant. Results of pairwise post-hoc comparisons indicate that clams from New Jersey were significantly younger at 60 mm than clams from the other three sites which were not significantly different. For age at 80 mm, the main effect of location ($F = 5.87$, $p = 0.0020$), covariate birth year ($F = 16.65$, $p < 0.0001$), and the interaction term ($F = 5.71$, $p = 0.0024$) also were all significant. At 80 mm, clams from New Jersey were significantly younger than clams from all other sites, and clams from Southern New England were significantly older than clams from the three other sites. For age at 90 mm, the main effect of location ($F = 25.71$, $p < 0.0001$) and the covariate birth year ($F = 77.83$, $p < 0.0001$) remained significant, but the interaction term was no longer so. A posteriori comparisons indicate that animals from the New Jersey and Georges Bank sites were significantly younger at 90 mm

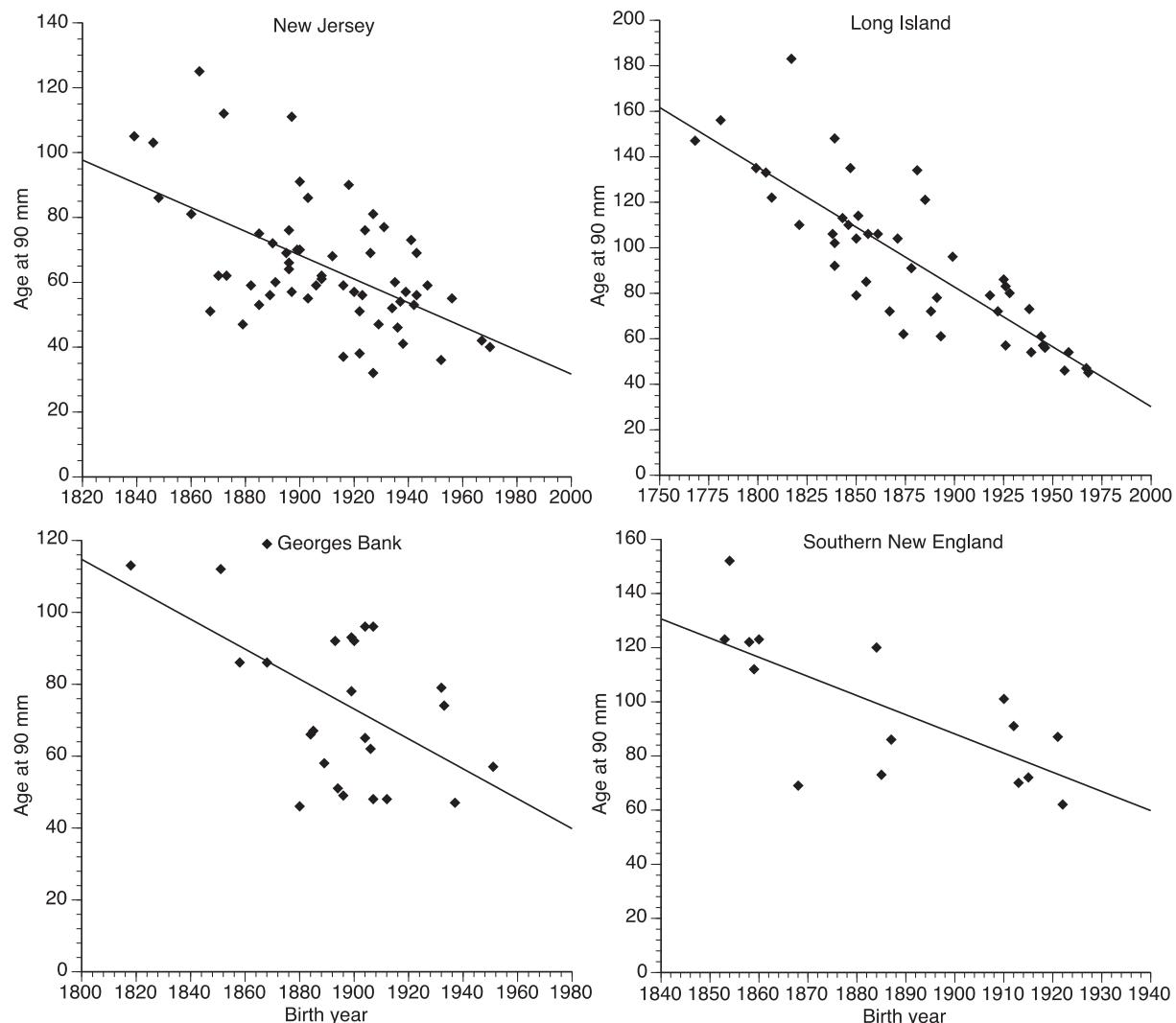


Fig. 3. Birth year versus age at 90 mm. Regression lines indicate significant correlations ($P \leq 0.05$).

than clams at the Long Island and Southern New England sites, but no significant differences in age at 90 mm existed between New Jersey and Georges Bank clams, nor did a significant difference exist between Long Island and Southern New England clams. Plots of the least squares means values and associated 95% confidence intervals for each site are shown in Fig. 7.

ANCOVAs using average growth rate to 60 mm and from 60 to 80 mm as dependent variables corroborate the results of the ANCOVAs with dependent variables of age at 60 mm and 80 mm. Results of the ANCOVA using growth rate from 80 to 90 mm as the dependent variable show a significant main effect of location and a significant birth year covariate [location ($F = 22.80$, $p < 0.0001$); birth year ($F = 39.54$, $p < 0.0001$)]. A posteriori comparisons indicate that ocean quahogs from New Jersey grew significantly faster from 80 to 90 mm than clams from the other three sites, and clams from Southern New England grew significantly slower than clams at all other sites. The average growth rate post-90 mm was also significantly influenced by location and birth year [location ($F = 23.48$, $p < 0.0001$); birth year ($F = 39.54$, $p < 0.0001$)]. The interaction term was not significant. Results of a posteriori comparisons suggest that clams from New Jersey had the fastest average growth rate at larger sizes than clams from the three other sites, whereas clams from Southern New England grew significantly slower than clams from both New Jersey and Long Island. Plots of the least squares means values and associated 95% confidence intervals for growth rates to each size are shown in Fig. 8.

3.3. Regression analysis

Multiple regression models for the New Jersey and Long Island sites suggest that the strongest predictors of birth year were length and average growth rate to 80 and 90 mm. These variables explained about 91% of the variation in predicting birth year at both sites (Table 1). At the Georges Bank and Southern New England sites, length, growth rate from 60 to 80 mm, and growth rate post-90 mm explained approximately 86% and 91% of the variability respectively. These results suggest that the ability to predict birth year at the two northern sites depends more on growth rates at larger sizes in addition to the total length of an individual, whereas the average growth rates from 60 to 90 mm in addition to the length are better predictors of birth year at the New Jersey and Long Island sites. These results recapitulate earlier trends exposed by Pearson correlations and ANCOVA. Fig. 9 shows the observed versus predicted birth year generated by the best three-variable model at each site.

Table 2 shows the results of the regressions to predict birth year for each site using only average growth rates to 60 and 80 mm (Fig. 10), and average growth rates to 60, 80, and 90 mm (Fig. 11). In the former, using only growth rates to 60 and 80 mm to predict birth year, significant regressions were produced for the New Jersey and Long Island locations only. Although significant, early growth rates only accounted for about 39% of the variation at the New Jersey site, but accounted for a higher proportion (58.6%) of the variation at the Long Island site.

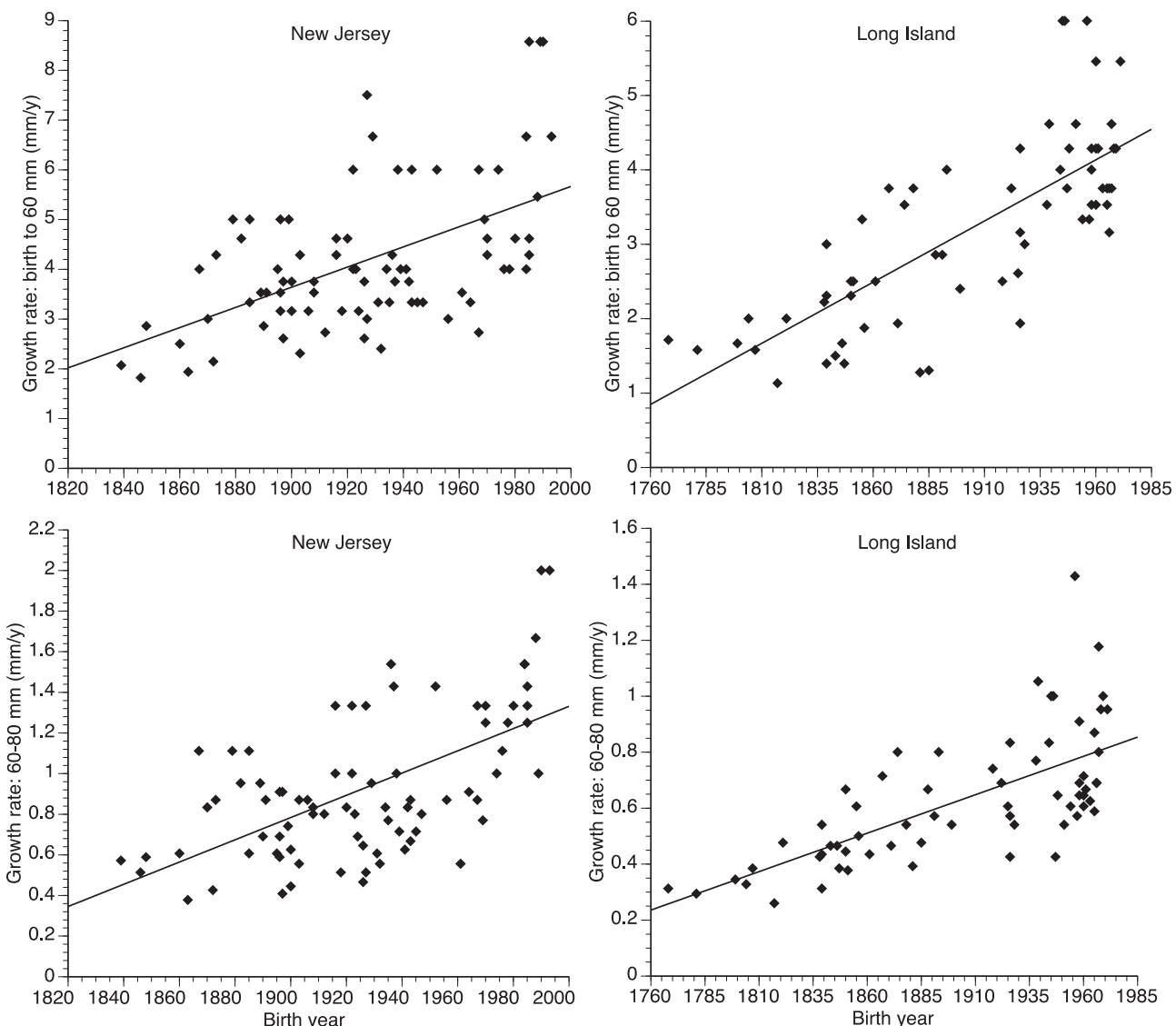


Fig. 4. Top: plots of birth year versus average growth rate from birth to 60 mm. Bottom: plots of birth year versus average growth rate from 60 to 80 mm. Regression lines indicate significant correlations ($P \leq 0.05$).

Nevertheless, the regression analysis indicates that a significant relationship exists between birth year and early growth rates at these two sites. In contrast, the two-variable models for Georges Bank and Southern New England not only were non-significant, but also lacked any ability to accurately predict birth year, as indicated by the very low R-square values.

The addition of average growth rate from 80 to 90 mm somewhat improves the Long Island model, increasing the R-square by 0.13. In the New Jersey model, the inclusion of this variable marginally diminishes the total variance explaining birth year, though this is likely due to the removal of animals < 90 mm in shell length from the model. The regressions for both the Long Island and New Jersey models remained significant, however. At the Southern New England site, the addition of this third variable results in a regression model accounting for about 51% of the variation in predicting birth year and a significant correlation, whereas the addition of this variable only modestly improves the R-square value for Georges Bank and the correlation remains non-significant. These analyses suggest that the inclusion of growth rate from 80 to 90 mm improves the ability to predict birth year at three of the four locations, excluding only Georges Bank, the most northern site.

4. Discussion

4.1. The relationship of growth rate and birth year

The variable growth rates of ocean quahogs to shell lengths of 80-mm throughout the range of this commercially valuable species has important implications for fishery management, as the fishing gear targets clams ≥ 80 mm in size. Based on Fig. 2, clams in New Jersey and Long Island are reaching a size that is available to the fishery typically between 10 and 20 years earlier than clams from the two more northeastern areas. Consider also that growth rates vary on decadal and longer time scales at the New Jersey and Long Island sites, with clams born more recently (e.g., 1960) reaching lengths of 80 mm at younger ages (e.g., average age of about 30 years in New Jersey and about 41 years in Long Island) than clams that recruited prior to 1900 (e.g., average age of about 49 years in New Jersey and 75 years in Long Island). As concerns exist about the ability of any long-lived species to recover in a reasonable amount of time should overfishing occur, this information suggests that the southern portion of the stock has higher resilience than the more northern portion and that this resiliency has increased substantively over time. Moreover, management based upon growth rates for the stock as a whole would underestimate the

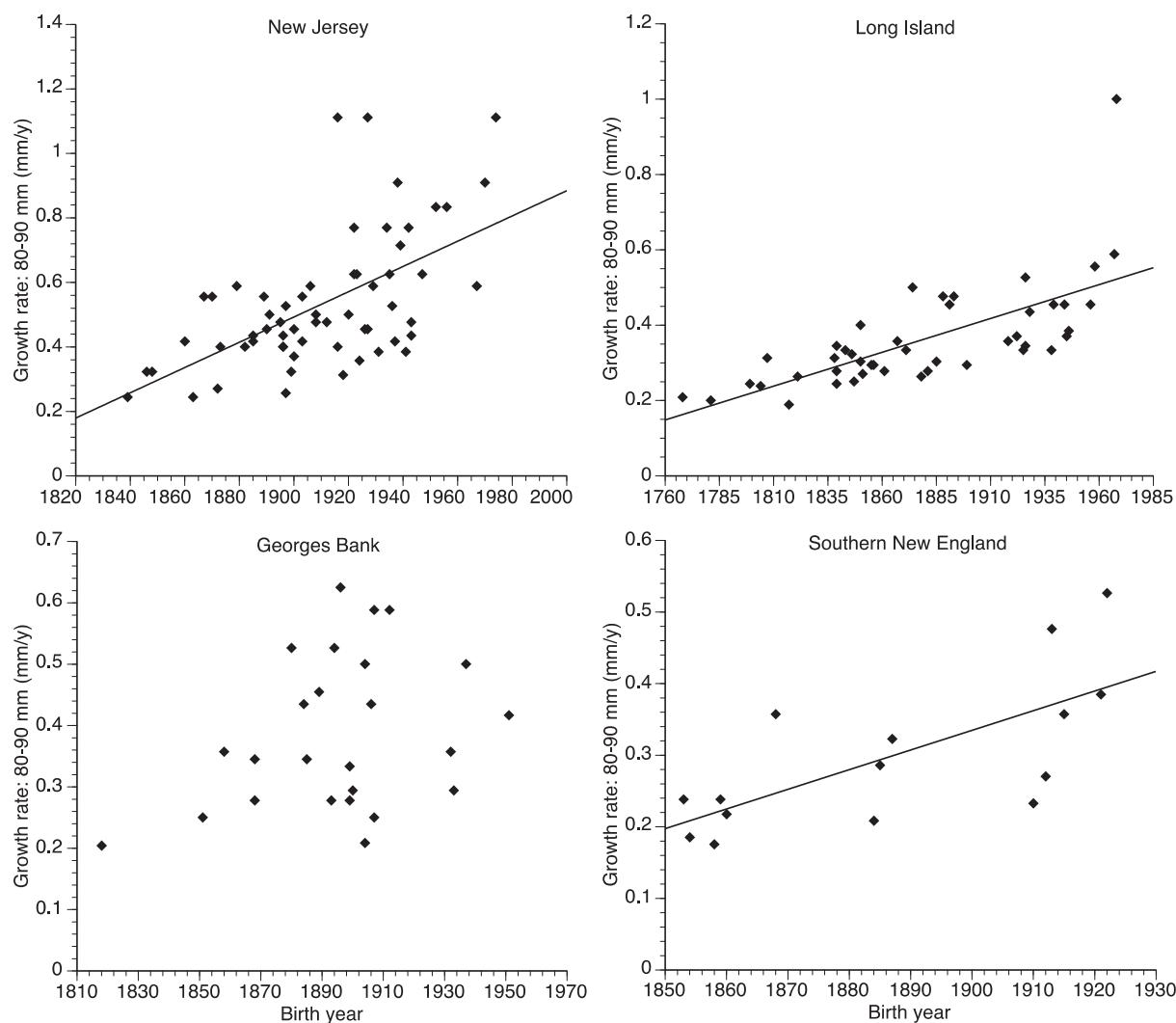


Fig. 5. Plots of birth year versus average growth rate from 80 to 90 mm. Regression lines indicate significant correlations ($P \leq 0.05$).

dynamics of the population anticipated for future years at least at the two more southern sites.

At the two northern sites, the significant correlation between birth year and age at 90-mm, as well as the average growth rate for animals exceeding 90 mm (dlen in Table 1, Fig. 6), is not entirely surprising, as a strong correlation exists between an individual's total shell length and the year the animal was born. The relationship between average growth rate for animals exceeding 90 mm and birth year would be anticipated, as ocean quahogs continue to grow as long as they are alive, so older animals should generally grow to a larger size than younger animals that have not had as much time to grow, and the amount of time that has passed between the time the animal reached 90 mm and the date of collection, being the denominator, will substantively influence the metric. This was supported in the regression analyses, as total shell length was the variable most strongly correlated with birth year at all four locations (Table 1). This likely explains why a significant relationship between birth year and average growth rate post-90 mm exists at the Southern New England and Georges Bank sites, but no relationship exists for the growth rates at 60 and 80 mm, as a multiple regression predicting birth year from just these two metrics has no predictive power (Table 2). However, one cannot discount that the existence of this relationship with birth year at larger sizes may also be due to increasing water temperatures, which may have resulted in increased growth rates at older ages for ocean quahogs born long ago that grew slower at younger ages while living in a cooler environment. The

growth rate from 80 to 90 mm may be instructive in this case. The correlation is significant for Southern New England (Fig. 5), and inclusion of the metric in a regression model provides considerably improved explanatory power, though still weak in comparison to that for the two southern sites (Table 2, Fig. 11).

Despite relatively low R-square values, examination of the significant regression produced using only early growth rates (Fig. 10) suggests that the two-parameter model provides a reasonably accurate prediction of birth year at the New Jersey and Long Island sites. If growth rates early in an individual's life had not varied over time, restriction of regression analysis to only early growth rates should result in an inability to predict birth year. The converse being true validates the inference seen in the correlation test results that the signal of time-dependent changes in early growth rates at the two southern sites was sufficiently strong to provide a reasonable estimate of birth year just from these metrics.

The lower R-square value at the New Jersey site in comparison to the Long Island site could be a consequence of the fact that this population is situated closest to the southern end of the species' range, where higher intra-decadal climate variability can be anticipated. Such variability would insert increased small-temporal-scale variation in growth rates, which would reduce the strength of the correlation while retaining a strong long-term temporal signal. The Long Island site, being north of Hudson Canyon, is in a distinctly different oceanographic regime less influenced by the vagaries of the Gulf Stream's influence on

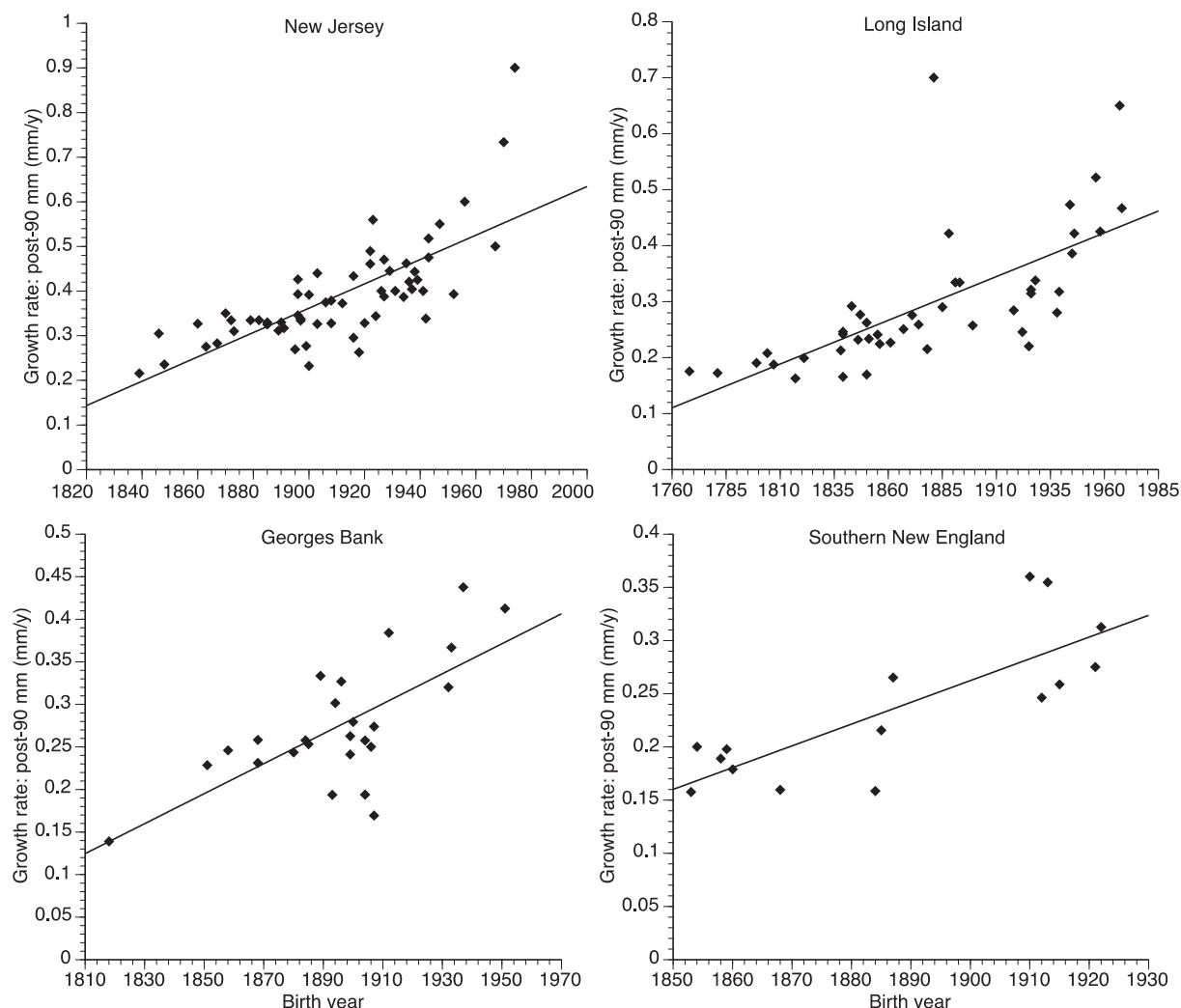


Fig. 6. Plots of birth year versus average growth rate post-90 mm. Regression lines indicate significant correlations ($P \leq 0.05$).

the continental shelf and the degree of southerly intrusion of the cold pool that permits ocean quahogs to survive at latitudes unusually far south for a boreal species (for more on the cold pool, see Bignami and Hopkins, 2003; Castelao et al., 2010; Lentz, 2017; for more on the Hudson Canyon as an oceanic barrier, compare NEFSC, 2017a, 2017b; see also Lucey and Nye, 2010; Zhang et al., 2015). Lesser intra-decadal climate variability may explain why of the two southern sites, the Long Island site had a better model fit than New Jersey, when the population at both sites responded relatively similarly to longer-term changes in oceanic climate.

Conversely, the Georges Bank and Southern New England sites lack a significant regression predicting birth year from early growth rate variables (Table 2); the regression fails to provide a discernable correlation between observed and predicted birth year (Fig. 10). The modest predictive capacity introduced by adding the growth rate from 80 to 90 mm to the regression for the Southern New England site emphasizes a strong southwest to northeast trend in the long-term influence of climate change on ocean quahog populations in this region earlier considered by Pace et al. (2017b). At the southern extreme, variation in growth rate over time exists in all phases of ocean quahog life, whereas on Georges Bank, little evidence exists for any differential in growth rate over the last ~200 years. In fact, Wanamaker et al. (2008) observed modest cooling of the Gulf of Maine by 1–2 °C over the last millennium (but see Moore et al., 2017), whereas Saba et al. (2016) suggest a high rate of warming potential in the Mid-Atlantic region (see

also Nixon et al., 2004) and Friedland and Hare (2007) document substantive temperature variations over the last 100+ years.

4.2. Regional difference in growth rate

Results of the ANCOVAs and post-hoc least squares means tests indicate that clams from New Jersey were significantly younger than all other sites when they reached 60 and 80 mm, and significantly younger than clams from Long Island and Southern New England when they reached 90 mm. At 90 mm, clams from Georges Bank were also significantly younger than clams from Long Island and Southern New England. Additionally, ocean quahogs from Southern New England were significantly older than those from the other three sites at 80 mm. This is best seen in Fig. 2 where clams born in New Jersey reached 80 mm at a younger age consistently across all birth years in comparison to the other sites.

Ocean quahogs from New Jersey also had significantly faster average growth rates than all other sites. ANCOVAs included birth year as a covariate; that is, growth rates were inherently faster at the southern sites regardless of the effect of birth year on growth rate. This is best seen in Fig. 4 where clams born in New Jersey grew at higher rates consistently across all birth years in comparison to the other sites. Clams from Southern New England grew significantly slower than those from the three other sites between 60 and 80 mm and 80 to 90 mm, whereas these animals only grew significantly slower than clams from

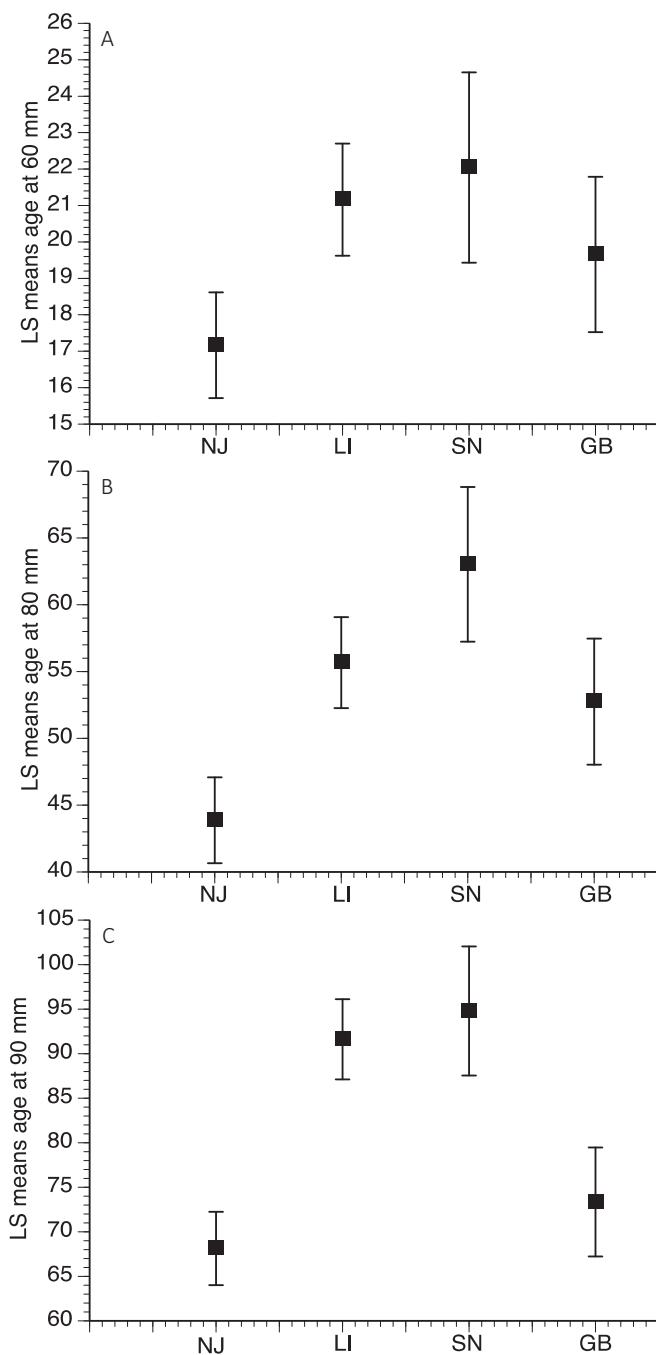


Fig. 7. Plots of the least squares means values and associated 95% confidence intervals for Jersey (NJ), Long Island (LI), Southern New England (SN), and Georges Bank (GB), for (A) age at 60 mm, (B) age at 80 mm, and (C) age at 90 mm. The values are not the true mean age at each size; rather they are the post-hoc least squares means values and associated confidence limits.

New Jersey and Long Island post-90 mm.

Interestingly, Long Island and Georges Bank tend to be paired in the results of the post-hoc tests (Figs. 7–8), as the only variable in which clams from these two sites significantly differed was age at 90 mm, yet these two sites displayed little difference in growth rate from 80 to 90 mm. Additionally, although ocean quahogs from Georges Bank were significantly older in age at 90 mm than those from Southern New England, clams post-90 mm exhibited no differences in growth rates at these two sites. Also of note is the absence of interaction effects between birth year and location at either the age of 90 mm, growth rates from 80 to 90 mm, or growth rates post-90 mm, suggesting that at

larger sizes, the effect of birth year was similar across all locations. Perhaps the strong correlation between shell length and birth year evident at all sites overrode the regional changes in growth rate with birth year noted at earlier life stages; alternatively, the inherently more modest growth rates of the adults may have limited the influence of changing environmental conditions at the southern sites.

4.3. Constraints in estimating population growth rates

Growth rates of ocean quahogs are known to be variable throughout the species range. Table 3 reports the parameters of the von Bertalanffy growth model for ocean quahogs from various studies, including parameters from the five oldest clams from the New Jersey, Long Island, and Southern New England sites in this study. Although this growth model has important weaknesses for this species (Pace et al., 2017a), its common use provides an opportunity for comparison. Evidence presented in this study, however, constrains comparisons on geographic scales or even site to site. Growth rates vary between animals born at different times in one location and, thus, parameter values for growth models, such as Brody's k , will also vary. Hence, the variation in growth rates between the populations summarized in Table 3 may result from the limited size and age ranges of the sampled animals, and not necessarily be representative of the larger age range of the species at the various sites.

Differences in the size of ocean quahogs that were aged also likely had an influence on the varying growth rates reported throughout the species' range. Murawski et al. (1982) sampled animals < 60 mm from Long Island. Kilada et al. (2007) estimated the age of animals < 86 mm. Pace et al. (2017a) focused only on animals ≥ 80 mm. In our study, substantive variation in growth model parameters can be anticipated depending on the birth year of the animal at the New Jersey and Long Island sites, and perhaps also at the Southern New England site. For the purpose of comparison to the Pace et al. (2017a) study using ocean quahogs from Georges Bank, values in Table 3 are derived from the five oldest clams from each site. Had the growth of younger clams been modeled instead, parameter values likely would have differed substantially.

In general, the uniqueness of ocean quahog growth and the sensitivity to climate change due to the long life span of the species, which exceeds the cycle period of commonly studied climate cycles (e.g., ENSO, NAO, AMO – Sutton and Hodson, 2003; Soniat et al., 2009; Nye et al., 2014) limits comparability of growth parameters. In fact, determining a population-level growth model depends upon variation in growth being a product of random variation between growth rates within and between cohorts, rather than directional change. That changing environmental conditions can modify growth model parameters within the time span of the life of a long-lived species is already well described for Atlantic surfclams, *Spisula solidissima* (Munroe et al., 2016; Chute et al., 2016) and other bivalve species (Brey et al., 2011). The much longer life span for ocean quahogs assures that any population with animals living through periods of climate change will be composed of animals with varying growth parameters, making a population estimate potentially illusory and certainly limiting between-population comparisons.

4.4. Origin of growth rate variation

Temperature is a primary determinant of growth in bivalves, being a strong effector of filtration and ingestion rate, respiration rate, and gametogenesis (e.g., Hofmann et al., 2006; Flye-Sainte-Marie et al., 2007; Munroe et al., 2013). Growth rate is a product of a balance between ingestion and respiration, often referred to as "scope for growth". The concept of "degree day" is often invoked to express the quasi-additive nature of temperature over time in determining growth rate. Respiratory rate rises with increasing temperature, in general following a Q_{10} relationship. Powell and Stanton Jr. (1985) reviewed bivalve

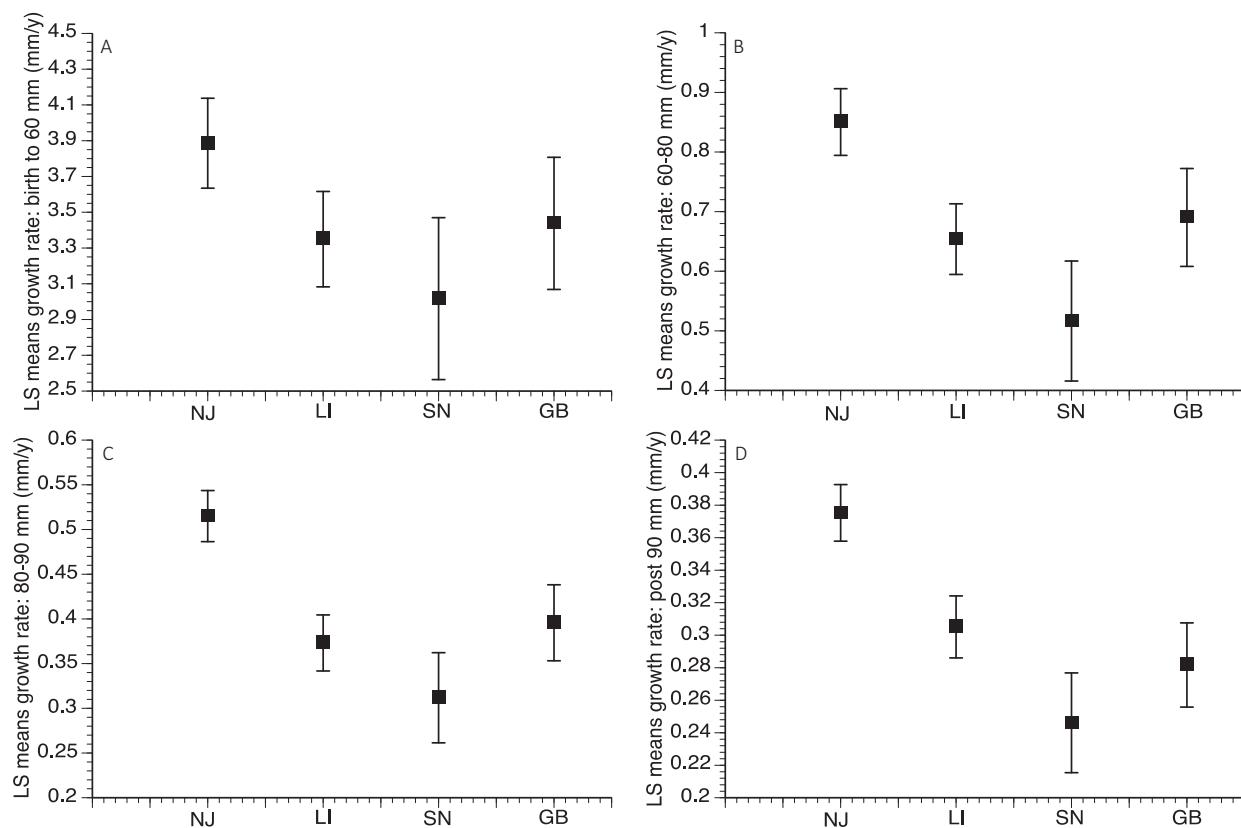


Fig. 8. Plots of the least squares means values and associated 95% confidence intervals for New Jersey (NJ), Long Island (LI), Southern New England (SN), and Georges Bank (GB), for average growth rates: (A) birth to 60 mm, (B) 60 to 80 mm, (C) 80 to 90 mm, and (D) post 90 mm. The values are not the mean age at each size; rather they are the post-hoc least squares means values and associated confidence intervals.

Table 1

Model selection results for each site using maximum R-squared selection to predict birth year using length (len), average growth rate birth to 60 mm (d60), 60–80 mm (d80), 80–90 mm (d90), and post-90 mm (dlen).

Candidate model	R square	C _p	p-value
New Jersey			
Birth year ~ len	0.6241	377.2133	< 0.0001
Birth year ~ len + d80	0.8370	122.4907	< 0.0001
Birth year ~ len + d90 + d80	0.9153	30.0737	< 0.0001
Birth year ~ len + dlen + d90 + d80	0.9285	16.2522	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9386	6.0000	< 0.0001
Long Island			
Birth year ~ len	0.6228	244.2283	< 0.0001
Birth year ~ len + d80	0.8956	25.4769	< 0.0001
Birth year ~ len + d90 + d80	0.9137	12.8192	< 0.0001
Birth year ~ len + d90 + d80 + d60	0.9266	4.3747	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9271	6.0000	< 0.0001
Georges Bank			
Birth year ~ len	0.3609	166.5788	0.0001
Birth year ~ len + d80	0.7692	42.3623	< 0.0001
Birth year ~ len + dlen + d80	0.8594	16.4636	< 0.0001
Birth year ~ len + dlen + d90 + d60	0.8934	7.9490	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9062	6.0000	< 0.0001
Southern New England			
Birth year ~ len	0.3752	226.5912	0.0011
Birth year ~ len + d80	0.8066	57.6249	< 0.0001
Birth year ~ len + dlen + d80	0.9099	18.7007	< 0.0001
Birth year ~ len + dlen + d90 + d80	0.9343	11.0409	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9520	6.0000	< 0.0001

respiratory rates, including the temperature dependency and the respiration rate of ocean quahogs has received targeted attention [Taylor and Brand, 1975; Begum et al., 2009]. Ingestion is a product of food

supply and filtration rate. Filtration rate rises with increasing temperatures to some optimal point whereupon it rapidly declines (e.g., Munroe et al., 2013). This left-skewed parabolic relationship dictates that the practical thermal limits are primarily determined by the impact of rising temperature on filtration rates [e.g., Narváez et al. 2015; see also Woodin et al., 2013]. This temperature-dependent physiology of bivalves is understood, sufficiently so as to sustain a large number of predictive population dynamics models (e.g., Hofmann et al., 2006; Flye-Sainte-Marie et al., 2007; Munroe et al., 2013).

Studies at different locations throughout the ocean quahog's range suggest that local temperature typically explains only about 10–30% of interannual shell growth variability (Schöne et al., 2003; Butler et al., 2010; Butler et al., 2013; Marchitto et al., 2000; but see evidence for even higher explanatory power provided by Marali and Schöne, 2015; Reynolds et al., 2017). Although this degree of explanatory power seems small, it likely identifies a key parameter leading to differential growth rates observed by these authors and is preferred in this study as the likely explanation for the observed long-term increases in growth rate. The temperature effect on growth inferred, however, appears to be much stronger than recorded in previous studies. In comparison to previous studies, the two southernmost sites sampled, off New Jersey and Long Island, are near the southern range boundary for this species and distinctly further south than any other location where ocean quahogs reach high abundance. Thus, temperature change in this region peaks near the maximum temperature conducting rising feeding rates. Ocean quahogs are noteworthy in having higher Q₁₀s than is typical for bivalves, reaching values of 3–4 (Begum et al., 2009), which sensitizes this species to small changes in temperature. Thus, in comparison to ocean quahogs in more northern climes, one might expect a temperature signal in the region studied here overriding other environmental factors influencing growth, and that is precisely what appears to be the case, as the 150+ year rise in growth rates documented at the two

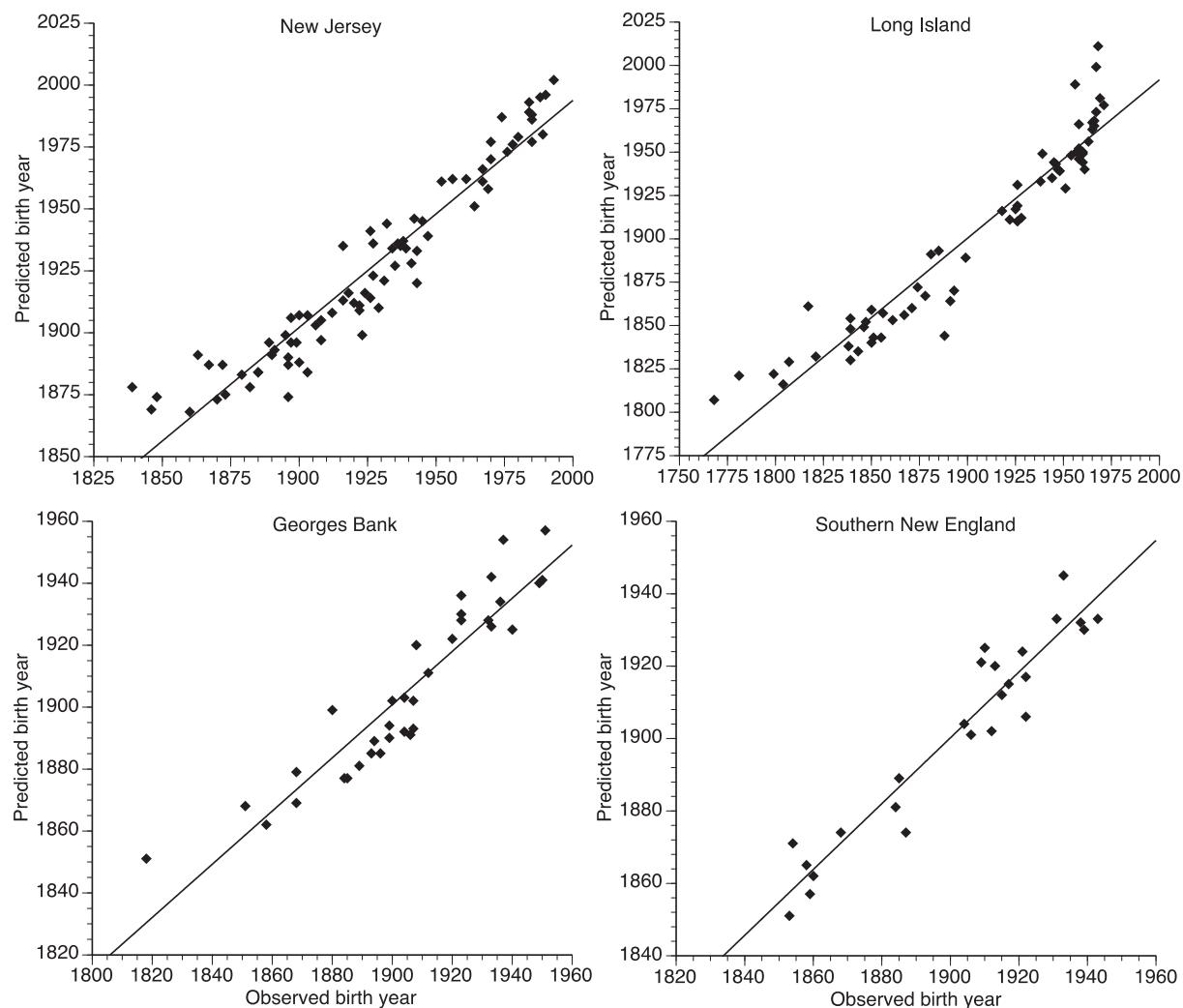


Fig. 9. Plots of observed versus predicted birth year based on the best 3 variables in the five variable regression models in Table 1. Regression lines indicate significant correlations ($P \leq 0.05$).

Table 2

Regression results for the two and three variable models to predict birth year using the average growth rate birth to 60 mm (d60) and 60–80 mm (d80), and for the three-variable model, 80–90 mm (d90).

Model	R squared	C _p	p-value
NJ			
Birth year ~ d60 + d80	0.3897	3.0000	< 0.0001
Birth year ~ d60 + d80 + d90	0.3798	4.0000	< 0.0001
LI			
Birth year ~ d60 + d80	0.5861	3.0000	< 0.0001
Birth year ~ d60 + d80 + d90	0.7189	4.0000	< 0.0001
GB			
Birth year ~ d60 + d80	0.0172	1.3022	0.6516
Birth year ~ d60 + d80 + d90	0.2800	4.0000	0.0702
SN			
Birth year ~ d60 + d80	0.0416	1.0008	0.6264
Birth year ~ d60 + d80 + d90	0.5058	4.0000	0.0446

southern sites is unlikely to be explained otherwise. In addition, analyses described here included a focus on growth rates of young animals including the juvenile phase of growth. Net growth efficiency is high in juvenile bivalves (e.g., Vahl, 1981; Hofmann et al., 2006; Begum et al., 2010) magnifying the potential influence of small environmental changes on growth rate. We note that long-term trends of increasing

growth rates with increasing temperature are not unprecedented in long-lived species (Davi et al., 2015; Moore et al., 2017). Ocean quahogs are unique, however, in that a long-term time series of early growth rates, to our knowledge, has not been shown previously for any animal species.

Environmental factors besides mean annual temperature such as food availability (e.g., Witbaard, 1996; Begum et al., 2009; Ballesta-Artero et al., 2017) likely also have an effect on growth rates and combined with temperature may explain the large disparity in maximum size of individuals at different sites; for example, the largest ocean quahog retrieved from New Jersey was 125-mm in shell length, whereas at the Southern New England site, the largest clam observed was only 108-mm, with only six individuals ≥ 105 -mm encountered in the population sample. Furthermore, the age of animals at various sizes differed between sites, with the youngest ocean quahogs at each length typically from the New Jersey site, and the oldest typically belonging to Southern New England. These differences were evident in the correlation tests and confirmed in regression and ANCOVA analysis.

As the most southern sampling site, the New Jersey site probably has had the warmest mean annual bottom temperatures, which could facilitate rapid growth, as well as growth to larger size maxima. Moreover, temperature also has an effect on the length of the growing season (Schöne et al., 2005b; Friedland and Hare, 2007) and on food supply, both of which can influence temporal trajectories of population metrics (system memories - see Soniat et al., 1998) on as yet

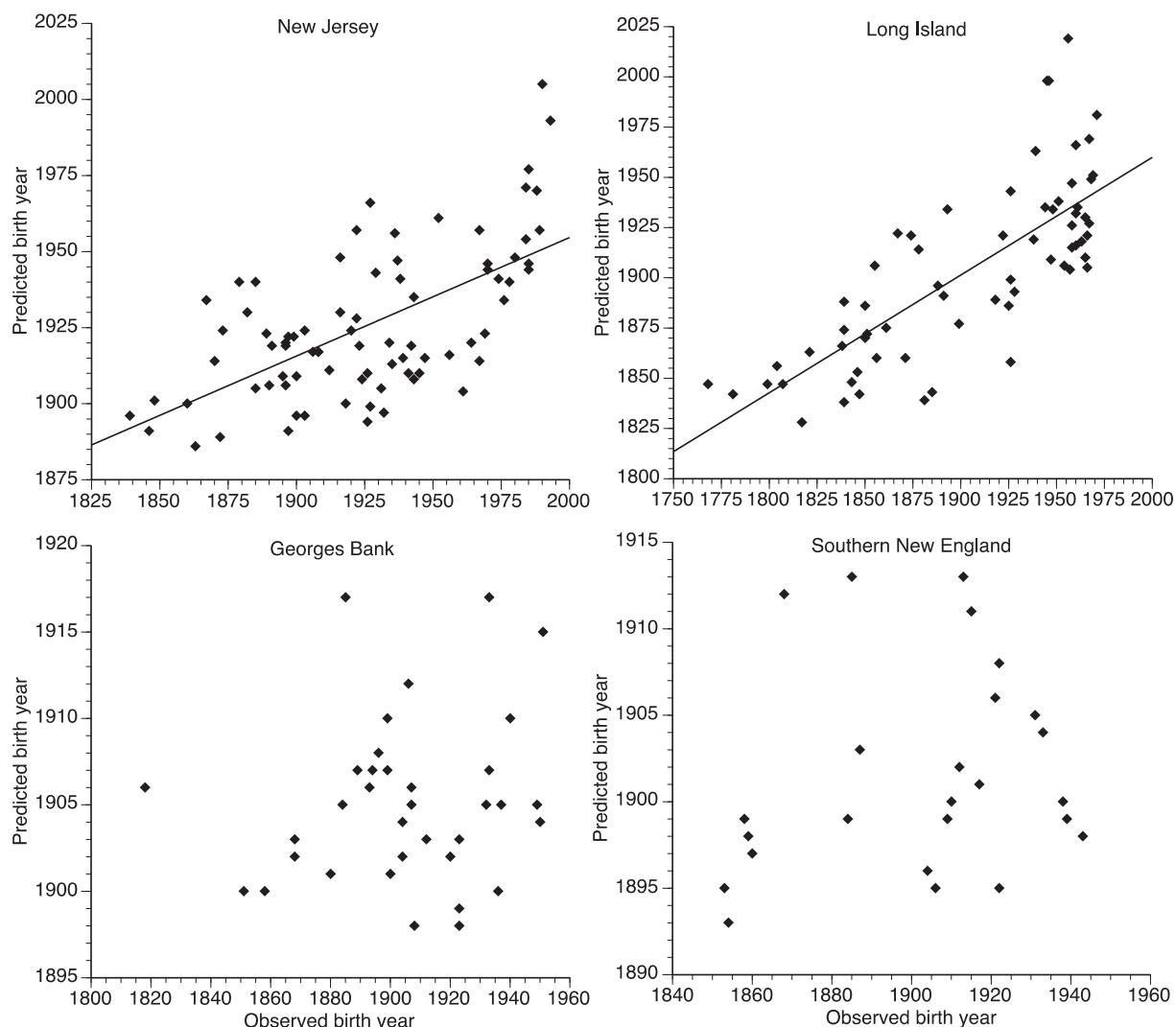


Fig. 10. Plots of observed versus predicted birth year based on the regressions shown in Table 2 using only early growth rates (birth to 60 and 60–80 mm). Solid lines indicate significant regressions from multiple regression models.

indeterminate, but multi-year, time scales. The northwest Atlantic continental shelf, in particular the New York Bight and Georges Bank, are among the most productive regions in the world (O'Reilly and Busch, 1984); accordingly, differences in primary production throughout the Mid-Atlantic may help explain the differences in growth between the four sample populations in this study. According to a report by Witbaard et al. (1999) in a study in the North Sea, primary productivity was considered to be the most important determinant of growth rate. Ballesta-Artero et al. (2017) found that in northern Norway, chlorophyll-a concentration was the main driver of valve gaping. Similarly, Lewis et al. (2001) suggested that the fast growth of ocean quahogs from Georges Bank was likely a result of the high productivity in the Georges Bank region. Perhaps this may help elucidate why in this study, animals from Georges Bank had similar ages-at-size, growth rates, and maximum observed shell lengths as animals from Long Island. Possibly, changes in temperature have resulted in the changing relationship between birth year and age-at-size and growth rate at the Long Island site, whereas at Georges Bank, the growth rates similar to those observed in Long Island may be a due to the fact that Georges Bank is and has likely been a more productive region over the histories of these populations. What is clear is that, despite a range of studies on the physiology and behavior of this species (e.g., Taylor and Brand, 1975; Mann, 1982; Oeschger and Storey, 1993; Begum et al., 2009), we still do not have a physiological model that can accurately

recapitulate the growth trajectory of this species in the way that is feasible for many other bivalves (see earlier references).

One important unknown is the influence of ocean quahog density on growth rate. Dense populations of bivalves are known to compete for food, thereby limiting growth rate (Powell et al., 1995; Fréchette and Daigle, 2002; Freitas et al., 2009). Ocean quahogs are considered to be near carrying capacity throughout their U.S. range today (NEFSC, 2017a) and this has likely been true for over half of the population's history since initial colonization in the late 1700s/early 1800s (Pace et al., 2017b). Thus, some influence of population density on growth rates might be anticipated. Evidence does not support such an influence, however. Lowest growth rates are recorded from New Jersey and Long Island early in the population's history when population densities were likely much lower (Pace et al., 2017b) and increasing population density on Georges Bank over the last 100+ years has not had any discernable influence on growth rates early or late in life. Pace et al. (2017b) consider the influence of the fishery at these sites, concluding that the fishery has exerted little influence on the species' population dynamics. In brief, the fishing mortality rate has been well below the natural mortality rate over the history of the fishery (NEFSC, 2017a) and the animals supporting the correlations between birth year and growth rate were nearly all born and grew to market size prior to the inception of the fishery; accordingly, the influence of changes in population density is an unlikely factor influencing the variations in

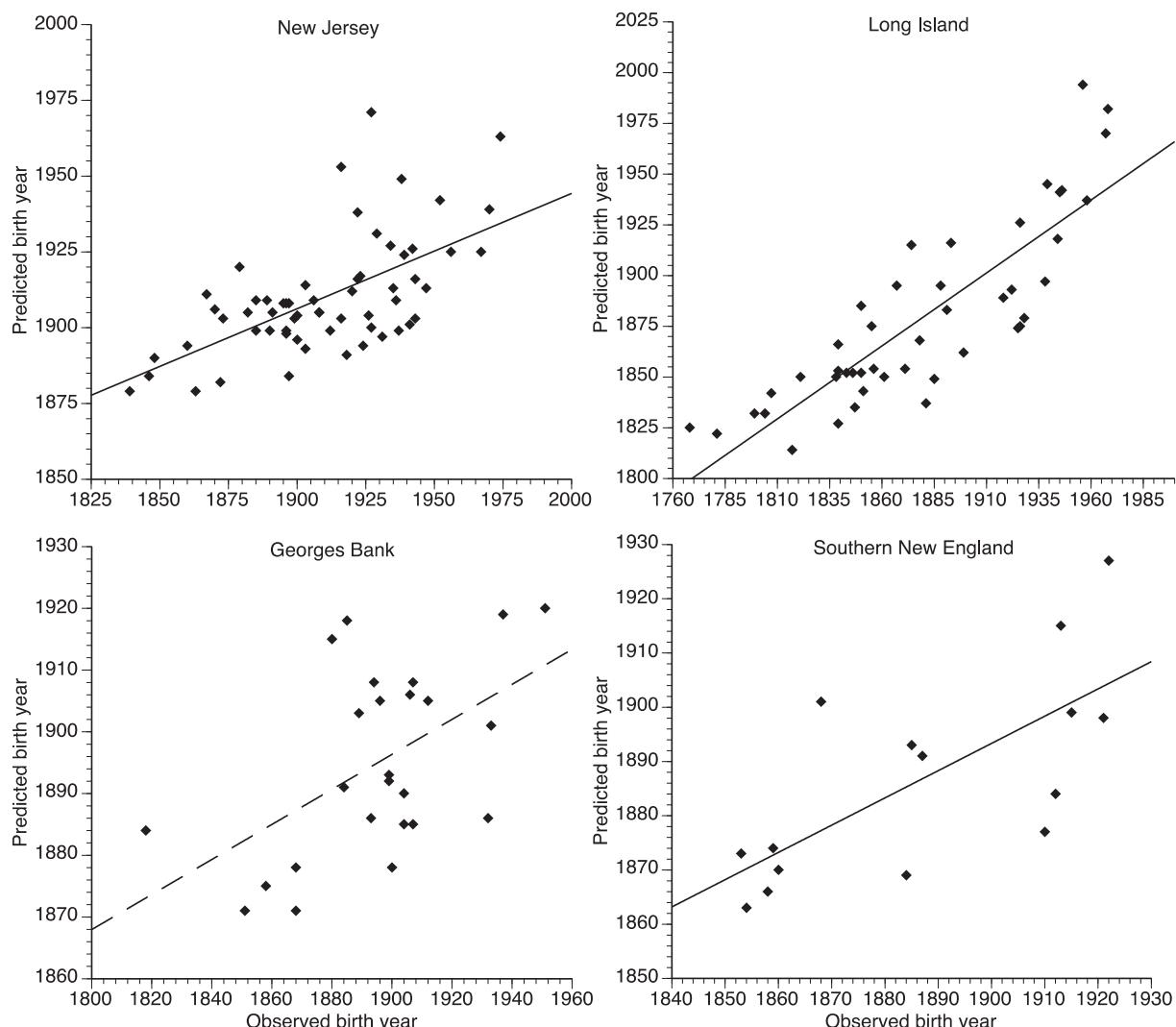


Fig. 11. Plots of observed versus predicted birth year based on the 3-variable regression models in Table 2. Solid lines indicate significant regressions from multiple regression models. Georges Bank regression (dashed line) not significant at $\alpha = 0.05$ (Table 2).

Table 3

Von Bertalanffy growth parameters for ocean quahogs from previously published studies and this study. Parameters from this study and Pace et al. (2017a) used only the five oldest animals at each site.

	L_{∞} (mm)	k
Long Island (Murawski et al., 1982)	107.6	0.02
Kiel Bay (Brey et al., 1990)	93.6	0.07
Mid-Atlantic Bight (NEFSC, 1995)	97.3	0.03
Georges Bank (Lewis et al., 2001)	97.6	0.06
Iceland (Thórarinsdóttir and Jacobson, 2005)	99.9	0.02
Iceland (Kilada et al., 2007)	92.5	0.03
St. Mary's Bay (Kilada et al., 2007)	87.6	0.05
Sable Bank (Kilada et al., 2007)	90.48	0.05
Belfast Lough (Ridgway et al., 2012)	93.7	0.03
Georges Bank (Pace et al., 2017a)	101.9	0.02
New Jersey (this study)	115.3	0.02
Long Island (this study)	104.73	0.01
Southern New England (this study)	94.62	0.03

growth rate as a function of birth year reported here.

5. Conclusions

Interpreting temperature effects on growth rates of ocean quahogs

throughout the history of the population is infeasible, as bottom water temperature records do not extend back to the time when the most recent colonization by this species began in the northwest Atlantic (Hulme and Jones, 1994; Hanna et al., 2004) and oxygen isotopic calibration (e.g., Weidman et al., 1994; Schöne et al., 2005a) is not yet available. Pace et al. (2017a) suggested that the most recent initial ocean quahog colonization on the continental shelf of the U.S. east coast co-occurred with the ending of the Little Ice Age. A dynamic explanation of this event remains unclear, as the location of the broodstock for initiating this range shift is unknown. Powell et al. (2017) document an offshore shift in range on Georges Bank; Zhang et al. (2015) describe a net down-coast larval drift for Atlantic surfclam larvae that might suggest a northern and/or inshore originating stock, but a reconstruction of the hydrodynamics of this time on the Mid-Atlantic continental shelf remains unavailable. Regardless of the source dynamics, the timing of this colonization coincides with a report by Moore et al. (2017), which presented evidence of a significant warming trend in the northwest Atlantic Ocean beginning during the middle of the 19th century, the time period concurrent with the end of the Little Ice Age (Schöne et al., 2005c; Mann et al., 2009; Cronin et al., 2010). Moore et al. (2017) show this warming trend continuing through to the present time. The warming of the northwest Atlantic may explain the significant correlation between birth year and the age at which individuals reach 60, 80, and 90 mm in shell length at the New Jersey and

Long Island sites, as these two sites are closer to the southern end of the species range than the Georges Bank and Southern New England populations. Increased bottom water temperatures could facilitate faster growth directly through higher filtration rates or indirectly through increased food supply, which may explain why ocean quahogs born more recently are growing faster than those born long ago. Birth year had little influence on the age-at-size at the two northern sites, however, with the modest exception of clams 90 mm in length. As water temperatures continue to increase, it is possible that changing growth rates will become evident at smaller sizes in future decades within the Georges Bank and Southern New England populations. Nevertheless, the Moore et al. (2017) temperature proxy comes from the Labrador Sea, well north of Georges Bank, so the minor or absent temperature signal in the Southern New England and Georges Bank populations seems unexpected. Reconstructed bottom water temperatures from 1875 to 1983 using *A. islandica* specimens from Georges Bank (Marsh et al., 1999) confirm the absence of a signal of increasing temperatures on Georges Bank, however.

Regardless of the mechanism, growth rates of ocean quahogs from the New Jersey and Long Island sites have clearly increased through time, with the age at which animals reaching 60, 80, and 90 mm decreasing as birth years advanced to recent years. Correspondingly, the growth rates to 60, 80, 90, and post-90 mm were all negatively correlated with birth year; that is, younger clams grew significantly faster than older clams at a comparable size born decades previously. This relationship was only evident at the age at which animals reached 90 mm at the Georges Bank and Southern New England site. This has important implications for fishery management, as ocean quahogs are becoming available to the commercial dredge in the southwestern region of the Mid-Atlantic Bight faster than they have in the past. These results also pose interesting questions on the mechanism behind the spatially and temporally variable growth rates of ocean quahogs throughout the range of this species. In particular, trends in ocean quahog growth parallel the rise in ocean temperatures after the Little Ice Age in the Mid-Atlantic Bight southeast of southern New England, yet demonstrate no evidence of such a rise in the Southern New England and Georges Bank region, which would suggest a differential response of ocean circulation and its control of bottom water temperature in this region over the last 200+ years.

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